Phytoplankton plasticity drives large variability in carbon fixation efficiency

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Key Points:
- Basin-scale high-resolution simulation of flexible phytoplankton C:N ratios
- Large C:N variability revealed at mesoscale, between trophic regimes and seasons
- This damps carbon sequestration variability at all scales

Supporting Information:
- Text S1

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Phytoplankton plasticity drives large variability in carbon fixation efficiency

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Abstract Phytoplankton C:N stoichiometry is highly flexible due to physiological plasticity, which could lead to high variations in carbon fixation efficiency (carbon consumption relative to nitrogen). However, the magnitude, as well as the spatial and temporal scales of variability, remains poorly constrained. We used a high-resolution biogeochemical model resolving various scales from small to high, spatially and temporally, in order to quantify and better understand this variability. We find that phytoplankton C:N ratio is highly variable at all spatial and temporal scales (5–12 molC/molN), from mesoscale to regional scale, and is mainly driven by nitrogen supply. Carbon fixation efficiency varies accordingly at all scales (±30%), with higher values under oligotrophic conditions and lower values under eutrophic conditions. Hence, phytoplankton plasticity may act as a buffer by attenuating carbon sequestration variability. Our results have implications for in situ estimations of C:N ratios and for future predictions under high CO_2 world.

1. Introduction

Marine primary production in surface waters is limited by nutrient availability with nitrate being the proximate limiting nutrient over most part of the ocean [*Tyrrell*, 1993; *Arrigo*, 2005; *Moore et al.*, 2013]. The efficiency of the biological carbon pump is determined by the amount of carbon that can be fixed given the available stock of limiting nutrient (assimilation ratio). Up to now, most biogeochemical ocean models have used constant C:N ratio (both for biomass and assimilation), based on Redfield stoichiometry [*Redfield*, 1934]. For instance, most models used in the Coupled Model Intercomparison Project 5 consider a constant C:N stoichiometry of 6.6 molC/molN or 7.62 molC/molN [*Bopp et al.*, 2013]. Such models hence assume a constant carbon fixation efficiency relative to nitrogen.

However, numerous observations have revealed large plasticity of phytoplankton physiology [*Rees et al.*, 2001; *Geider and La Roche*, 2002; *Arrigo*, 2005; *Klausmeier et al.*, 2008; *Martiny et al.*, 2013a]. As a consequence, C:N ratios of assimilation and organic matter can deviate from Redfield stoichiometry up to 40% [*Sambrotto et al.*, 1993; *Banse*, 1994; *Kortzinger et al.*, 2001; *Koeve*, 2004; *Martiny et al.*, 2013a, 2013b; *Moore et al.*, 2013]. Under nutrient-limited conditions, flexible C:N ratios allow the production of a relatively higher amount of organic carbon than would be expected from nitrogen uptake according to Redfield stoichiometry. This process is commonly referred as "carbon overconsumption" [*Toggweiler*, 1993]. Assuming a fixed C:N stoichiometry could then lead to biases in carbon fixation estimates from nutrient uptake. Additionally, previous in situ and modeling studies have suggested that C:N stoichiometry of phytoplankton and assimilation can strongly vary from mesoscale [*Rees et al.*, 2001; *Omta et al.*, 2007] to seasonal [*Fernandez et al.*, 2005] and regional scales [*Kortzinger et al.*, 2001; *Koeve*, 2006; *Martiny et al.*, 2013b] (Figure 1).

In this context, the aim of the present study is to assess the variability of the phytoplanktonic C:N ratio and of the carbon fixation efficiency in the ocean and to identify their spatial and temporal scales of variations. For that, we used a high-resolution biogeochemical model resolving various scales from small to high, spatially and temporally, in order to quantify and better understand this variability.

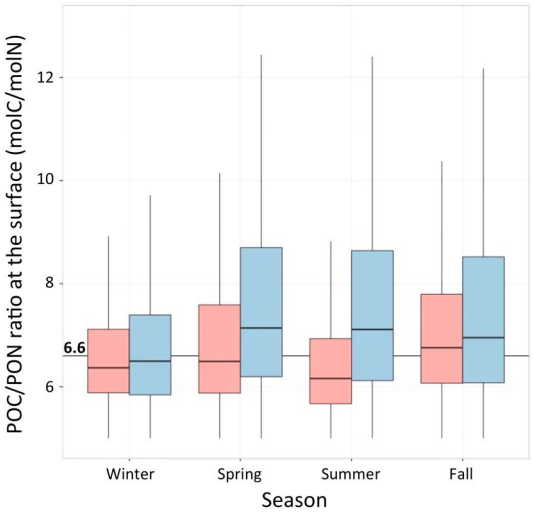

Figure 1. Regional and seasonal variability of the POC/PON ratio in the ocean. Particulate organic carbon (POC) and nitrogen (PON) data encompass 38,468 punctual observations from 20° and poleward in both hemispheres. Oligotrophic regions (in blue) and eutrophic regions (in pink) have been distinguished from the median value of PON (1.07 μmol/L). Boxplots indicate median, first, and third quartile ("hinges") and 95% confidence interval of median ("notches"). The canonical Redfield value of 6.6 molC/molN is indicated. Data have been gathered by *Martiny et al.* [2013b].

2. Methods

We used an idealized submesoscale-permitting configuration of the northwestern Atlantic ocean, reproducing oligotrophic subtropical and productive subpolar regimes. The primitive equation model Nucleus for European Modelling of the Ocean [*Madec*, 2008] was used in conjunction with the biogeochemical model LOBSTER (Lodyc Ocean Biogeochemical System for Ecosystem and Resources) [*Lévy et al.*, 2012a]. The model domain was a rotated rectangle, bounded by vertical walls and by a flat bottom that covered the latitudinal range 15°N to 50°N (Figure 2). The circulation was forced by a repeating annual cycle of zonal wind and buoyancy fluxes, which varied seasonally in a sinusoidal manner between winter and summer extrema. The horizontal resolution was submesoscale permitting (1/54°). The biogeochemical model LOBSTER solves for phytoplankton, zooplankton, detritus, dissolved organic matter, nitrate, and ammonium [*Lévy et al.*, 2012a, 2012b]. More detailed information about the model configuration, closures, and parameters can be found in *Lévy et al.* [2010, 2012a].

A new version of the LOBSTER model was developed with flexible C:N and Chl:C ratios for the phytoplankton (model version P2.5 in *Ayata et al.* [2013]). Phytoplankton growth is represented following *Geider et al.* [1998] so that nitrogen and carbon assimilations are decoupled, allowing a flexible C:N ratio for phytoplankton. Nutrient uptake is constrained by nutrient availability and phytoplanktonic C:N ratio. Carbon fixation is constrained by light and phytoplanktonic C:N ratio. Photoacclimation is accounted for using a diagnostic chlorophyll:carbon ratio as a function of light and nutrient limitation [*Geider et al.*, 1998; *Ayata et al.*, 2013]. Zooplankton, detritus, and dissolved organic matter are only represented in nitrogen currency, as in the original LOBSTER model. This means that when the phytoplankton is eaten or dies, the fate of the lost part of carbon is not represented in this model. The equations and the default parameters used in this version of the LOBSTER model with flexible C:N ratio can be found in the supporting information. The solution obtained with the physical model at 1/54° was degraded down to 1/9° [*Lévy et al.*, 2012b] in order to run off-line this new version of the biogeochemical model over one climatological year. The spin-up state obtained with the original LOBSTER model [*Lévy et al.*, 2010, 2012a] was used as initial conditions.

We defined the C:N assimilation ratio as the ratio between the net carbon uptake (primary production minus respiration) and the nitrogen uptake. The carbon fixation efficiency was then defined as the relative difference between the C:N assimilation ratio and the Redfield C:N ratio of 6.6 molC/molN [*Redfield*, 1934]. The carbon fixation efficiency hence corresponds to the percentage of carbon overconsumption/underconsumption.

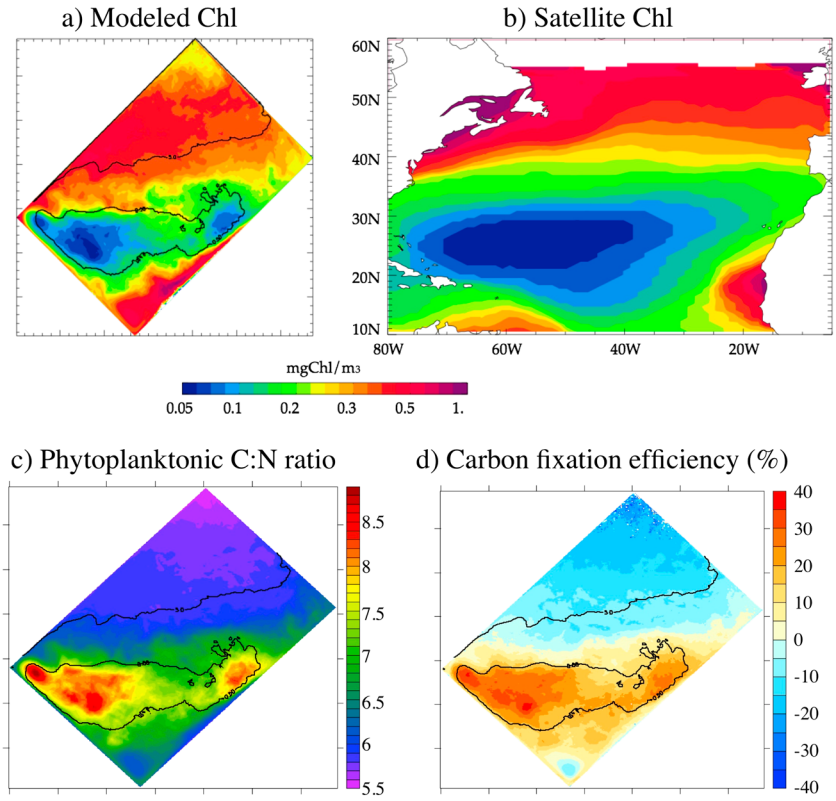

Figure 2. (a) Annually averaged surface chlorophyll concentration simulated by the model. (b) Annually averaged surface chlorophyll concentration observed by satellite in the North Atlantic (GlobColour product). (c) Annually averaged value of surface phytoplankton C:N ratio (molC/molN). (d) Annually averaged carbon fixation efficiency at the surface, calculated as the relative difference between the C:N assimilation ratio and the canonical Redfield ratio (6.6 molC/molN). Two regions have been defined from the nitrate concentration at 50 m and are delineated with black lines: one eutrophic region in the north (>5 mmol/m^3) and one oligotrophic region in the south (<0.5 mmol/m^3).

The biogeochemical model was able to reproduce realistic values of surface chlorophyll (Figures 2a and 2b) and regional variability of biogeochemical processes, with a southern oligotrophic region and a northern eutrophic region (delineated with black lines in Figure 2).

3. Variability of the Phytoplanktonic C:N Ratio

3.1. Description of the Various Scales of Variability

At basin scale, the annual mean value of phytoplanktonic C:N ratio at the surface is close to the canonical Redfield value of 6.6 molC/molN (averaged value of 6.5 molC/molN). At regional scale, the phytoplanktonic C:N ratio simulated by the model is higher in the southern oligotrophic region than in the northern eutrophic area, with annually averaged values of 7.7 and 5.8 molC/molN, respectively (Figure 2c).

The phytoplanktonic C:N ratio also varies at seasonal scale, with higher values during spring and summer (Figure 3a). Additionally, seasonal variations are stronger in the oligotrophic area (seasonal averages between 6.75 molC/molN in winter and 8.82 molC/molN in summer) than in the eutrophic region (between 5.30 molC/molN in winter and 6.21 molC/molN in summer).

The large variability in C:N values in the oligotrophic area (vertical bars in Figure 3a) is due to variability at smaller spatial and temporal scales (Figure 3c). Indeed, mesoscale structures are also responsible for sharp variations in phytoplanktonic C:N ratio at the surface. For instance, at the horizontal scale of an anticyclonic eddy of about 100 km of radius, the C:N ratio of the phytoplankton can vary from 11.8 molC/molN within the eddy to 6.6 molC/molN outside (Figure 3c).

At all scales, surface phytoplanktonic C:N ratio can be strongly anticorrelated with nutrient concentration (averaged correlation of −0.7371 using log-transformed nitrate concentration, p value < 0.001). For instance,

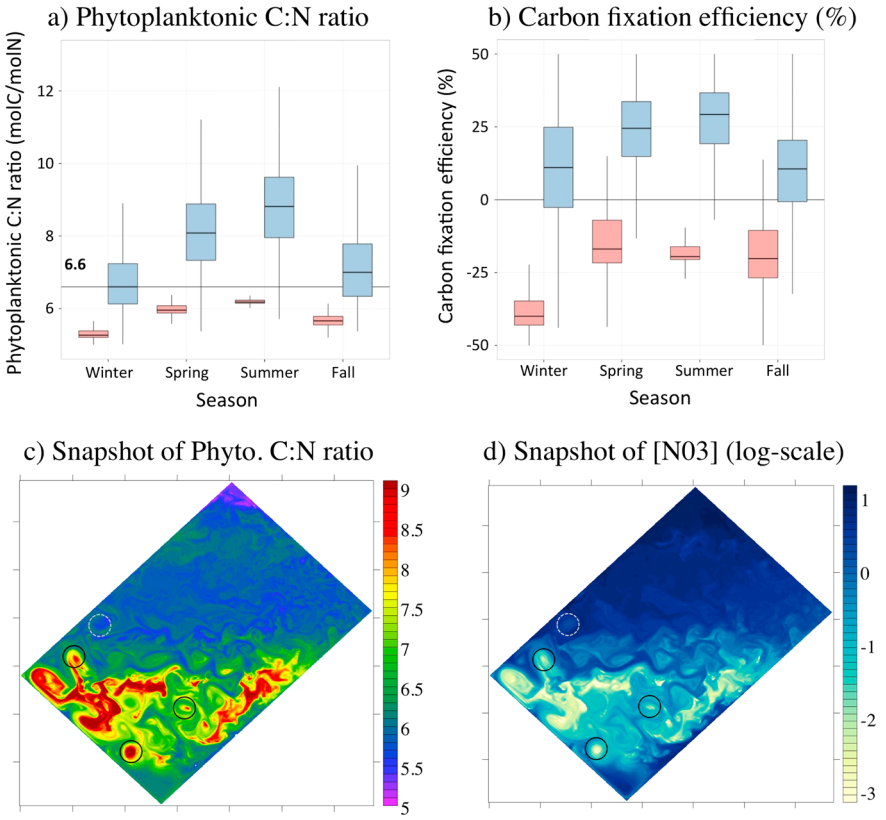

Figure 3. Seasonal and regional variability at the surface of (a) phytoplanktonic C:N ratio and (b) carbon fixation efficiency (overconsumption and underconsumption) and snapshots in spring of surface (c) phytoplanktonic C:N ratio (molC/molN) and (d) nitrate concentration [NO_3] using a logarithmic scale (log(mmolN/m^3)) (16 April). Two regions are considered: a eutrophic region in pink and an oligotrophic region in blue; the delineations of these regions are indicated on Figure 1. Black continuous circles indicate examples of eddies with high phytoplanktonic C:N ratio and low nitrate concentration. The dashed grey circle indicates one example of eddies with low phytoplanktonic C:N ratio and high nitrate concentration.

strong anticorrelations can be observed at mesoscale within filaments and eddies (Figures 3c and 3d). Hence, the variability of phytoplanktonic C:N ratio is mainly driven by nitrogen availability, known to vary from mesoscale to regional scales [*Mahaffey et al.*, 2004; *Moore et al.*, 2013].

4. Carbon Fixation Efficiency

4.1. Scales of Variability

C:N assimilation ratio exhibits the same patterns of variability at regional scale, seasonal scale, and mesoscale as phytoplankton C:N ratio, but with slightly higher values. For instance, at the scale of the whole basin, mean annual value of C:N assimilation ratio reaches 7.1 molC/molN at the surface. One explanation for higher assimilation ratio could be the vertical mixing of cells from deeper layers that have relatively lower C:N stoichiometry. Such cells would then be able to have a high assimilation ratio but a relatively lower biomass ratio. Indeed, assimilation C:N ratio responds instantly to environmental conditions (nutrient concentration) and physiological state (biomass C:N ratio), whereas phytoplankton C:N ratio integrates in time the history of the phytoplankton cells.

At regional scale, a higher assimilation ratio was simulated in the southern oligotrophic region than in the northern eutrophic region, with mean surface values of 9.0 molC/molN and 5.8 molC/molN, respectively. This variability drives fluctuations in the carbon fixation efficiency at regional scale, from −23% in the eutrophic area to +22% in the oligotrophic area (Figure 2d). Carbon fixation efficiency also varies at seasonal scale and mesoscale, with higher values during spring and summer (Figure 3b).

4.2. Comparison With Field Observations

The high spatial variability at mesoscale should be kept in mind when looking at point observations of phytoplanktonic C:N ratios in the ocean. Indeed, in addition with sampling difficulties and measurement biases, this high variability at different spatial and temporal scales makes the in situ estimation of C:N ratio for phytoplankton and assimilation extremely challenging.

In situ assimilation ratios are most frequently estimated from the measurement of the consumptions of nitrate and dissolved inorganic carbon (corrected from sea-air exchanges and carbonate formation by calcifying organisms). Such measurements thus correspond to the whole community net assimilation ratio, whereas our estimations relate to phytoplankton net assimilation ratio. Nevertheless, and despite the scarcity of in situ data, simulated ranges of variations of biomass and assimilation ratios are coherent with observations [*Rees et al.*, 1999; *Kortzinger et al.*, 2001; *Koeve*, 2004, 2006; *Martiny et al.*, 2013a] (Figure 1). For instance, from radio and stable isotope tracers, *Rees et al.* [1999] observed variations of C:N assimilation ratios from 2.5 to 9 molC/molN in spring in the Celtic Sea, with a similar range of variation recorded by *Kortzinger et al.* [2001] in the northeast Atlantic (from 5–6 molC/molN in spring to 10–16 molC/molN in summer). At regional and seasonal scales, higher C:N assimilation ratios were observed at subtropical latitudes than at subpolar latitudes in the northeast Atlantic, with opposite trends in nutrient availability [*Kortzinger et al.*, 2001; *Koeve*, 2004; *Fernandez et al.*, 2005; *Koeve*, 2006]. At mesoscale, C:N assimilation ratios ranging from 8 to 14.9 molC/molN were reported at the surface in summer within an anticyclonic (clockwise) mesoscale eddy of about 60 km of diameter in the northeast Atlantic [*Rees et al.*, 2001].

A first estimate of carbon overconsumption was given by *Sambrotto et al.* [1993] between 36% and 81%, although this estimation was later debated [*Kortzinger et al.*, 2001; *Koeve*, 2004]. Although estimated from phytoplankton net assimilation ratio instead of community net assimilation ratio, our results are in agreement with those observed by *Kortzinger et al.* [2001] and *Koeve* [2004]: carbon overconsumption is about 20% during oligotrophic period (i.e., with considerably lower value than the ones estimated by *Sambrotto et al.* [1993]), and carbon underconsumption occurs during eutrophic condition.

4.3. Potential Consequences on Carbon Fixation

Variations in carbon fixation efficiency may have important impacts on ocean biogeochemistry. Indeed, our result indicates that flexible C:N stoichiometry may reduce the differences between relatively highly productive regions and oligotrophic regions. Indeed, it would relatively increase production when/where it is low (because nutrients are scarce) and conversely decrease production when/where it is high (because nutrient are not limiting). Plasticity of phytoplankton stoichiometry could then act as a buffer by decreasing carbon sequestration variability at all scales.

A relative excess of carbon assimilation (also sometimes referred as luxury consumption) can lead to the exudation of transparent exopolymer particles (TEPs) formed from the dissolution of polysaccharides [*Engel et al.*, 2002]. Since TEP excretion could favor aggregation, particle formation, and hence export, flexibility in C:N assimilation ratio could then lead to strong spatiotemporal variability in carbon export, with relatively higher export under low nutrient condition. The variability of carbon export, which occurs at all spatial and temporal scales [*Resplandy et al.*, 2012], could then be damped by phytoplankton plasticity.

These results have strong implications for global ocean models, especially in the context of climate change and future high CO_2 world, as increased C:N ratios (both for biomass and assimilation), increased carbon consumption, and decreased nutritional values of organic matter are expected [*Burkhard et al.*, 1999; *Riebesell et al.*, 2007; *Finkel et al.*, 2010; *Taucher et al.*, 2012]. Our results suggest that phytoplankton flexibility may act as a buffer to environmental changes, and increased C:N ratios could allow maintaining high carbon fixation efficiency even when/where nutrients become limiting.

5. Limits of Our Study

The main limit of our study is the relatively simple formulations we have used. First, we considered only one phytoplankton type. Indeed, observed changes in C:N biomass ratios may also be related to change in the phytoplankton species assemblage [*Donald et al.*, 2001; *Arrigo*, 2005; *Martiny et al.*, 2013a]. Hence, the mean C:N ratio of small eukaryotic phytoplankton is lower than for the prokaryote

Prochlorococcus (8.7 ± 0.3 molC/molN versus 10.1 ± 0.5 molC/molN) [*Martiny et al.*, 2013b]. Second, the fate of the overconsumed carbon is not modeled. Simulating the whole carbon cycle would allow to estimate the proportion of carbon that would be grazed, excreted as TEP, respired, and finally exported in the deep ocean. For instance, C:N ratio of particulate matter may evolve along the water column due to differential remineralization. Additionally, explicit representation of carbon excretion as TEP could even increase carbon overconsumption estimates. Although using a relatively simple biogeochemical model, our study highlights the importance of flexible stoichiometry in primary production estimates and suggests that a flexible C:N ratio should at least be simulated for phytoplankton, specially as the computation costs are becoming less and less limiting. Indeed, one of the main reasons most marine biogeochemical models still do not take into account flexible C:N stoichiometry is the computer time/power required when the number of state variables increases. Therefore, we strongly advocate for implementing variable C:N ratio in ocean biogeochemical models, at least for the phytoplanktonic compartment. It would then be interesting to adapt our basin-scale study to a marine ecosystem model able to simulate several phytoplankton functional type with variable C:N ratios in order to describe the impact of variable C:N ratio on higher trophic levels and export. To do so, flexible C:N ratios could, for instance, be implemented for different plankton size classes [*Talmy et al.*, 2014].

6. Conclusion

Our modeling study suggests that phytoplankton C:N ratio is highly variable at all spatial and temporal scales, ranging from mesoscale to regional scale and that carbon fixation efficiency varies accordingly. This wide range of spatial and temporal scales at which C:N ratios vary make their in situ estimation extremely challenging. Since the main driver of these variations is nitrogen availability, the highest carbon fixation efficiency occurs under oligotrophic conditions. Conversely, flexible C:N ratio is also responsible for low carbon fixation efficiency under eutrophic conditions. Hence, phytoplankton plasticity acts as a buffer by decreasing production variability. In the future, oligotrophic regions are expected to extend, hence decreasing carbon export. However, our study suggests that this decrease could be partially compensated by an increase in C:N ratio.

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